With the Author's Comp[ts]

A

RE-STATEMENT OF THE CELL THEORY,

WITH APPLICATIONS TO THE

MORPHOLOGY, CLASSIFICATION, AND PHYSIOLOGY OF PROTISTS PLANTS, AND ANIMALS.

TOGETHER WITH AN

HYPOTHESIS OF CELL-STRUCTURE AND AN HYPOTHESIS OF CONTRACTILITY.

WITH PLATE

By PATRICK GEDDES.

Reprinted from the Proceedings of the Royal Society of Edinburgh, vol. xii., 1883–84.)

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A Re-Statement of the Cell Theory, with Applications to the Morphology, Classification, and Physiology of Protists, Plants, and Animals. Together with an Hypothesis of Cell-Structure, and an Hypothesis of Contractility.* By Patrick Geddes. (Plate IV.)

(*Communicated 3d December* 1883.)

Position and Importance of the Cell Theory in Morphology.—Vast though is the literature of vegetable and animal morphology, it becomes more readily grasped than that perhaps of any other science, when we classify it in relation to the few great works which initiated and for ever mark the successive waves of advance. Thus of the early pre-morphological or encyclopædic stage, when materials were being little more than heaped together, the works of Pliny or Gesner may be taken as types, to which the other encyclopædias of Natural History by Joinston, &c., furnish at first mere supplements. The *Systema Naturæ* of Linnæus closes the old and marks a new era, and initiates that systematic enumeration of the flora and fauna of the globe which has since made such vast progress. All subsequent systematic literature, no matter how important, no matter how much exceeding in quantity of new forms, involves no essential, no qualitative advance: thus the greater part of the proceedings of such

* Prelim. Note in *Zool. Anzeiger*, No. 146, 1883.

Societies as the Zoological or the Linnean, such new and important faunistic literature as that contained in the magnificent volumes of the "Challenger" Expedition, or even the greatest systematic works, find their highest place not as superseding, but as supplementing the fundamental classic of Linnæus. Similarly all works of detailed anatomical research united with exact comparison and clear generalisation, are in botany simply to be regarded as supplementary to the little work in which Antoine de Jussieu founded the Natural System, or in zoology to the *Règne Animal* of Cuvier, himself also an intellectual heir of Vesalius. Embryological literature in like manner finds its place in the appendix and commentary to the works of Robert Brown or Von Baer respectively; at the head of all investigations of serial homologies stands Goethe's memorable essay *On the Metamorphoses of Plants;* while all evolutionary literature may be arranged round the works of Lamarck and Darwin. The morphological investigator, unless claiming to initiate some new line of thought, has thus to take his place simply as an assistant to one or more of a few immortal masters.

But the cell theory? This is apt to be excluded from general morphology altogether, and to have a separate subordinate province —of histology—erected for it, a vicious tendency, which although by no means fully adopted, still somewhat injures the continuity of treatment in the writer's recent essay on Morphology.* To ascertain its position, we must first briefly glance at its history.

Here the fundamental classic is undoubtedly the *Anatomie Générale* of Bichât, though in this the name of cell does not even occur, the "tissue" being assumed as fundamental. The analysis of the organism into definite structural components is, however, the main idea; after this the history of histology is little more than of accumulating observations with improving optical and technical appliances, until we come to Schleiden, who boldly referred all vegetable tissues to the cellular type, and the plant embryo to a single nucleated cell; while Schwann, by immediately extending the generalisation to the animal world, fully constituted the cell theory. This idea then is fundamental in morphology; for the innumerable species and genera of plants and animals made known under the leadership

* *Ency. Brit.*, xvi. p. 837; amended in German translation, *Jenaische Zeitschr.*, 1884.

of Linnæus, and the numberless anatomical resemblances and differences investigated by Cuvier and his disciples, become reduced to resemblances and differences in the details of structure and position of fundamentally similar unit masses; while the resemblances of development made known by embryologists become the connecting link between the cell theory and these generalisations of adul structure. It is not necessary to do more than merely allude to such applications of the cell theory, or to that of the study of pathological structure initiated by Goodsir and Virchow, or to that brilliant confirmation of the unity of the animal and vegetable cell which has lately been afforded by the detailed study of the processes of cell multiplication. Agassiz* was fully justified in the opinion that the most brilliant result of modern science was the ovum-theory, and thus it is beyond dispute that "in our own day, as in those of Bichât and Schwann, the labours of the histologist, when inspired by higher aims than that of the mere multiplication of descriptive detail, are of supreme morphological importance, and result in the demonstration of a unity of organic structure deeper even than any which we owe to Linnæus or Cuvier, Goethe or Geoffroy." †

Cell.—The position and importance of the cell theory being thus defined, the fundamental necessity for a precise conception of the cell itself will be sufficiently obvious. The early progress of this is well known; at first the vegetable cell-wall gave the type, while Schwann's cells were essentially nucleated vesicles with fluid contents. Dujardin described the "sarcode" of Foraminifera; Von Mohl discovered the "protoplasm" of the vegetable cell; while Max Schultze identified both as the same substance; showed it, and not the membrane to be essential; and gave an amended definition of the cell as a unit mass of nucleated protoplasm. For working purposes it is this conception which is generally accepted, and almost every dissertation or treatise upon the general questions of botany or zoology, histology or physiology, commences by postulating it, the amœba being most frequently taken as the standard type.‡

Unsolved Problems.—Such a conception of the fundamental

* *Essay on Classification.*

† "Morphology," *Ency. Brit.*, xvi. sec. 3, p. 840.

‡ Of this no better instance can be afforded than the introduction to the admirable *Manual of Physiology* of Dr Michael Foster.

cellular unit, however valuable, yet throws no light upon a large number of problems at present under dispute; and it is the aim of the present paper to draw attention to some of these, and by the aid of a re-statement of the cell theory (a new appendix as it were to the *Anatomie Générale*, or to the work of Schwann), to propose a solution of them.

The problems then which it is proposed to discuss may be briefly enumerated for convenience under separate heads, as follows:—

(1) The classification and affinities of the Protozoa.

(2) The classification and affinities of the Protophytes.

(3) The systematic position of the Myxomycetes and other peculiar forms.

(4) The acceptance or rejection of Hæckel's third intermediate sub-kingdom *Protista*.

(5) The phylogeny of the lower plants and animals, and their origin from one or several stocks.

(6) The relation of the Protophytes to the higher plants.

(7) The relation of the Protozoa to the higher animals.

(8) The morphological relations of plants to animals and their origin from a common stock, or from separate ones.

(9) The classification of animal tissues.

(10) The physiological rationale of changes of cell-form.

(11) A theory of the origin of sexual reproduction, and its relation to conjugation and other cases of cell union.

(12) The relation between normal and pathological tissues.

(13) The influence of the environment on the origin of organic forms.

(14) A theory of cellular variation (since the theory of descent involves a theory of variation, and all variations, normal and pathological alike) must ultimately be expressible in terms of cellular ones.

1. *Classification and Affinities of the Protozoa.*—The Protozoa have long been thrown into a few main groups, of which the *Rhizopoda*, embracing all essentially amœboid forms like the Protoplasta, Foraminifera, Heliozoa, and Radiolaria, and the Infusoria, including all those of permanent and usually ciliated type, are the oldest and most important. The position of the Gregarinida, of the Monads, and still more of forms like *Chlamydomyxa* and the Labyrinthulida,

or Hæckel's *Protomyxa*, is still disputed, nor is that of Rhizopods to Infusors, despite their more or less intermediate forms, as yet settled.

But our current conceptions of the groups of Protista are based upon their more prominent and permanent characters only. An infusorian is constantly thought of as a permanently ciliated or flagellate organism; a radiolarian is constantly described as a highly differentiated rhizopod, with two layers of protoplasm, a gelatinous envelope, yellow cells, and siliceous skeleton; or again its simpler ally the heliozoon is seldom or never thought of without its radiating pseudopodia with their peculiar axial filaments.

Yet such conceptions involve a morphological fallacy of the most serious kind. These are indeed the most highly differentiated, the most frequent, the most permanent, and therefore the most striking forms in which these organisms are known to us, but of late years it has been becoming more and more obvious that each of these well-known forms is at best but the most important stage of a life-history, during which the organism passes through one or more other phases of form, which may indeed be transitory, but thereby lose no whit of their morphological distinctness or importance.

Thus, thanks to the researches of Dallinger and Drysdale, Butschli, Savile Kent, and others,* we know that a monad is not a permanently flagellate form, but appears at one time encysted, at another becomes amœboid; the ciliated embryos of the Acinetæ have long been known,† while more recent investigations have established the multiplication of radiolarians by zoopores,‡ or the frequent union of several individuals of various species of Heliozoa§ or of Gregarines|| into a single mass. In short, the progress of recent research among these forms has largely lain in revealing the existence in even the most highly differentiated forms of a life-cycle of several distinct phases.

In lower forms more attention is paid to the whole life-cycle, yet not sufficiently so. The Amœba is still constantly spoken of as if its encysted stage were of no morphological interest, whereas no permanently amœboid form has ever been proved by continuous

* Savile Kent, *Manual of the Infusoria*. † *Ibid.*

‡ Brandt, *Monatsb. d. Berlin Akad.*, 1881.

§ Gruber, *Zool. Anzeiger*, No. 118, 1882.

|| Gabriel, "Z. Classif. d. Gregarinen," *Zool. Anzeiger*, 1880.

observation to exist; in the Gregarine, on the other hand, the amœboid state is often practically ignored by classifiers.

In the remarkable Protomyxa of Hæckel, however, we have an organism in which several phases of form are almost equally prominent, so that its description as an amœboid, or a ciliated or as an encysted organism, has been alike impossible. For here is no permanent highly differentiated form; but an eventful life-history in which one protean mass of protoplasm passes through a cycle of several distinct phases. Let us carefully examine then these phases, since light may thus be thrown upon the life-histories of the higher Protozoa already referred to.

Starting then from the encysted stage, in which a mass of protoplasm is surrounded by a dense envelope, we find that from this after a time (in which division of the protoplasm has in this case occurred), there issues a swarm of somewhat pear-shaped, naked, motile, flagellate organisms. After a brief period of active locomotion, these lose their flagellum and their permanent form alike, extrude pseudopodia, in short, melt down into amœbæ. After some period of amœboid life they flow together into a single protoplasmic mass—unite into a plasmodium, as it is termed, and this after another brief but remarkable period of locomotion and pseudopodial activity, settles down into a spheroidal mass; this re-encysts itself, and the whole cycle commences anew (Plate IV. fig. 1).

If now we make a diagrammatic representation of this life-history (or rather *form-history*, as it should more accurately be termed), of *Protomyxa*, exhibiting (1) the encysted, (2) the ciliated, (3) the amœboid, and (4) the plasmodial stages, we shall find that all those temporary phases of form observed among the higher Protozoa may at once be referred to one or other of these (figs. 3, 8). If this be so, those curious phenomena of the exhibition of ciliated forms by organisms usually of amœboid type like the Radiolarians, or of amœboid forms by organisms almost permanently encysted or motile, like Gregarines or Monads respectively, lose their anomaly, and come under a generalisation at once simple and comprehensive, viz., that a form-history essentially similar to that of *Protomyxa* (with blanks it is true, but blanks which the progress of discovery is constantly filling up, and may not unlikely almost wholly fill), may be sketched out for all the higher Protozoa. The same idea

may be better expressed in the statement that the higher Protozoa may be regarded as organisms of fundamentally Protomyxoid form-history, in which, however, some one phase has attained comparatively high specialisation and differentiation, together with relatively greater permanence. Or the same idea may be stated in the exactly converse way, that the Protozoa may be viewed as organisms of fundamentally Protomyxoid form-history, in which, however, one, two, or three of the phases become abbreviated into merely embryonic ones, or may even (by that shortening of development with which embryologists are so familiar in the higher organism) become completely suppressed.

Thus then, if illustration be needed, a Heliozoon differs from Protomyxa merely * in the higher differentiation and relative permanence of the amœboid phase of its life-cycle, since more or less brief encysted, ciliated, and plasmodial phases have all been observed. The more specialised but kindred Radiolarian seems to have lost its plasmodial phase; so too, perhaps, has the monad, while in the Gregarine only the ciliated state is wanting.

2. *Affinities of the Protophyta.*—Passing now to the second problem proposed at the outset, that of the affinities of the Protophytes, the same conception may be at once applied. Too much importance is here attached to the encysted phase, for the life-cycle is clearly apparent in many forms. Treviranus, in 1811, made the notable discovery that the spores of Confervæ move like Infusoria.† Many years later Unger described the same phenomena in *Vaucheria clavata*, as "the plant in the moment of transition to the animal,"‡ while Von Siebold and others argued against this essentially just view, with more ingenuity than soundness. The wide prevalence of this change is constantly being confirmed. Not only have we a thoroughly well-defined and constant cycle between the resting and the ciliated state, but we may fairly reckon the brief phase of inactivity, which so often is observable between the loss of cilia and the return to the encysted state (when the organism closely resembles

* The possession or non-possession of a nucleus is of course immaterial, so far as the form-history is concerned.

† Treviranus, *Beitr. z. Pfl. Physiol.*, Gött. 1811, p. 78.

‡ Unger, *Die Pflanze in Momente d. Thierwendung*, Wien, 1843. Siebold, *Dissert. de finibus int. reg. an. et reg. constit.*, Erlangen, 1844.

a contracted amœba), as representing the amœboid form. A distinct assumption of the amœboid state at the close of the ciliated one, is sometimes to be observed,—as lately by Reinke* in Bangia. And thus the cycle is complete, save only for the plasmodial phase.

The importance of this view for the Protophytes then, is scarcely less than for the Protozoa. With a tendency of the encysted state to predominance, more marked even than in the Gregarines, the other phases are by no means obliterated, and we thus—and only thus—obtain an intelligible explanation of that alternation between the resting and the motile phase which is so frequent and so characteristic. The inevitable applicability of this to classification, and the light it yields, will be sufficiently obvious. Without prematurely proposing a detailed classification, it will be obvious that we must regard those forms, which like *Torula*, exhibit only the resting state, not as primitive, but as exceedingly specialised, and those which exhibit more and more of the cycle as less so.

3. *Affinities of the Myxomycetes.*—Passing to the *Myxomycetes*, it will at once be evident, that unless the present theory can be entirely overturned, they have no place among the fungi proper—where it is the encysted phase that predominates, the others being greatly reduced or suppressed; but are in fact morphologically as remote from these as are the monads. The Myxomycetes must be placed next *Protomyxa*; in fact, *Protomyxa* is simply the least differentiated known Myxomycete. Their higher forms are interesting—first, in very frequently showing less of the ciliated stage, and secondly (a more important character, since here they are unique among living beings), in affording an enormous differentiation of their plasmodial stage; the complicated forms which many of them exhibit being simply those of their plasmodial froth, to which permanent shape is then given by the formation of a cellulose envelope. The resemblance to fungi is thus as purely superficial and adaptive as that, for instance, of Hydroids to Polyzoa, and, like it, is of physiological interest alone.

4. *The "Protista."*—The general non-adoption of Hæckel's proposal of a third intermediate *Regnum Protisticum*, has been due to three main reasons,—of which the first is that the proposal seems only to double the difficulty, since it does not enable us to distinguish

* *Mittheil. d. Zool. Stat. in Neapel.*, 1883.

Protista from animals on the one hand, or plants on the other; the second, closely related to the first, that Protista are too heterogeneous, and do not admit of exact definition; but the third and most potent reason has, however, simply been that excessive specialisation which allows most otherwise competent students of the Protozoa to remain in entire indifference to the Protophytes, and the even more general and deplorable ignorance of the Protozoa which prevails among microscopic botanists.

The present theory, however, does away with the apparent heterogeneity of the Protista. On the view that Protozoa and Protophytes alike exhibit more or less specialised and abbreviated forms of a common life-cycle, the thirteen groups of Hæckel* are seen to be but forms of one, and there remains absolutely no morphological reason for their continued separation (nor for that matter, any physiological reason either, were such considerations, irrelevant as they are to morphological taxonomy, any longer admissible). Nor is the objection of Huxley really valid. The limit between *Protista* and *Animalia* remains simply that between Protozoa and Metazoa; and that between Protozoa and Protophytes being given up, there remains no more difficulty of separating the higher plants than there was before—a difficulty which, however undoubted, is not increased by uniting the lower forms.

The thorough unity and naturalness of the Protista being thus obvious, they naturally fall into a series corresponding to the stages of the life-cycle. In the Schizomycetes and the Palmellaceæ the resting and motile stages are almost equally prominent, while in Gregarines, and still more in Desmids and Diatoms, and especially Saccharomycetes, the encysted stage predominates. The Protoplasta, Foraminifera, Heliozoa, and Radiolaria represent of course the predominatingly rhizopod or amœboid stage, while the Infusoria represent the ciliated, and the Myxomycetes, as has been said, the plasmodial.

It may at first sight seem as if the old grouping of Protophytes and Protozoa were not seriously modified, since the Protophyta always essentially corresponded to the series of generally encysted forms. And so far true; the encysted series may still be termed Protophytes without any serious harm. But it must be clearly

* *Die Protisten.*

observed that there remains not *one* morphological type merely, to be discriminated as Protozoa, but *three*—the ciliated, amœboid, and plasmodial,—all, indeed, physiologically analogous in exhibiting movements (a phenomenon of which pure morphology takes absolutely no cognizance), but as distinct in form from each other as from the encysted form. The utter confusion which has too long maintained as to the distinction of plant and animal life is thus seen to be due to the want of that discrimination of morphological from physiological considerations, which is now happily nearly complete in the study of higher organisms. In short, though the encysted and usually non-motile cells or cell-aggregates may be conveniently termed plants by the physiologist, and though usually non-encysted and motile cells or cell-aggregates may similarly be grouped as animals,—yet the morphologist, distinguishing form-history from life-history, must recognise among the Protista four main lines of differentiation, or four series, which may perhaps conveniently be termed *Protophyta*, *Rhizopoda*, *Ciliales*, and *Plasmodiales*. (See Plate IV. figs. 1–13 in first series.)

5. *Phylogeny of Protista.*—On this view also there is no necessity for the assumption lately coming into view of the origin of the Protista from several distinct stocks, or for accepting, with Bergh,* so specialised a form as *Peridinium* as a type of the primeval Protozoon, for all are naturally derivable from a simple Myxomycete or Protomyxoid ancestor. Of course, this view by no means excludes the possibility of the remoter and simpler Protamœboid progenitor assumed by Hæckel.

6. *Relation of the Protophytes to the Higher Plants.*—Transverse division may of course occur in the encysted, amœboid, or ciliated stage of the life-cycle of a cell. When this takes place chiefly in the encysted state the tough and coherent wall holds the resultant cell-aggregate together; this cell-aggregate soon becomes moulded by the force of the environment into some definite form; and what we term a vegetable organism (a Metaphyte corresponding to a Metazoon) is the result.

But the cells of our multicellular plant do not lose their tendency to cycle. Alike in linear, superficial, or solid aggregates, the cycle is

* Bergh, "D. Org. d. Cilio-flagellata," *Morph. Jahrb.* vii. 2; Abstract by T. J. Parker, *N. Z. Jour. of Sci.*, October 1882.

plainly seen: and it is scarcely necessary to remind the reader of the zoospores of a confervoid Alga, or of the similar mode of reproduction of an *Ulva*. It may be objected that here only two stages of the cycle are present; but a third, the amœboid, not uncommonly occurs, for that the brief quiescent state of the zoospore before re-encystment may fairly be considered amœboid, is demonstrated by such observations as those of Reinke,* who has lately figured a true amœboid stage in the settling zoospore of *Bangia*.

In Fucus, again, the ovum-cell has rejuvenesced, in other words has gone through an amœboid stage, while other cells rejuvenesce as antherozoids into the ciliated phase. In the terrestrial Archegoniata, too, we have the same phenomena; even in the Phanerogams, condemned as all their cells seem to perpetual incarceration, there remains one fleeting and imperfect recapitulation of the cellular life-cycle in the embryonic rejuvenescence of the pollen grain and ovum cell (see fig. 15).

7. *Relation of Protozoa to Higher Animals.*—If transverse division occur in the ciliated state, the new cells must necessarily almost invariably separate, must row apart, and thus it is natural that only comparatively few and transitory cases of ciliated aggregates are known. In the amœboid state, however, the aggregate produced by division remains much more readily in continuity, and it would thus seem much more probable that the Metazoa should originate from Protista in which the amœboid stage was somewhat more permanent and more subject to division, than from the ciliated forms, as has sometimes been suggested, particularly for the sponges.

8. *Common or separate Descent and Affinities of Animalia and Vegetabilia.*—If the preceding facts and deductions be accepted, it need only be briefly pointed out, that the affinities of plants and animals are far closer than botanists and zoologists are generally accustomed to assume, since both are descended from a Protomyxoid ancestor, and may, in fact, from our present point of view, be described not merely, as the common phraso goes, as amœboid or encysted cell-aggregates, but as aggregates of Protomyxomycetes, variously grouped and arranged indeed, but never so highly specialised as to lose all traces of their individual ancestral life-cycle. The notion of *three* kingdoms of nature—animal, vegetable, and

* *Op. cit.*

mineral—"that disastrous philosophic and scientific aberration" bequeathed by the alchemists to the last encyclopædist of Gesner's school, and unfortunately adopted and sanctioned by Linnæus, has not of course been seriously adopted by any philosophical biologist of the century; hardly the narrowest specialist among zoologists or botanists any longer seriously doubts the validity of the classification of natural objects into two groups only—inorganic and organic—yet, at the same time, the vicious results of the earlier dogma still everywhere survive, and indeed necessarily so. For the unity of plant and animal life requires morphological demonstration, and that more precise than has hitherto been afforded by merely separating off the lowest plants and animals into a third still heterogeneous group of *Protista*. This deficiency is supplied by the present argument, for if the Protista, the Vegetabilia and the Animalia have indeed been correctly interpreted, as somewhat variously specialised cell-aggregates derived from an ancestral Protomyxomycete, their consolidation into a single kingdom is a matter of course. In one edition of the *Systema Naturæ*, Linnæus clearly recognised the fundamental unity of plants and animals, by uniting them in opposition to the non-living world (*Conserta*) as *Organisata*, and this term it is accordingly not only convenient, but necessary forthwith to revive.

9. *Morphological Classification of Animal Tissues.*—Histologists are accustomed to recognise three main groups of animal tissues. Thus Cornil and Ranvier * distinguish (1) connective tissues, in which the cells are united and separated by a substance of characteristic form and properties; (2) muscular and nervous tissue, in which the cells have undergone extraordinary modifications, both structural and functional; (3) epithelial tissue, in which the cells possess a regular and constant evolution.

In this classification, however, as in so many others, morphological and physiological characters are not kept distinct. In briefly glancing at morphological characters only, it is evident we may best approach the problem by first noticing some of those cellular transformations made known by the recent students of embryology. Histogenesis must underlie histology.

An ovum is at first a naked amœboid cell, then assumes the encysted state, then segments into an aggregate of amœboid cells; this

* *Manuel d'Histologie Pathologique*, i. p. 11, Paris, 1881.

becomes perhaps a ciliated morula, this again a gastrula, with ciliated ectoderm and amœboid endoderm; this may settle down as in sponges, its cells re-cycling anew, the ectodermic layer becoming amœboid, the endodermic ciliated (fig. 18). The endodermic cells remain permanently more or less amœboid, as the recently much investigated phenomena of intercellular digestion have so clearly established. The amœboid ectodermic cells, on the other hand, may give rise to muscle—and a muscle is but an amœba elongated so as permanently to contract along one line; on the other hand, they may pass into a quiescent state, or throw out encysting material, which may either enclose them individually, as in Ascidians, or form a collective external envelope, as in Arthropods. The mesodermic cells may either remain unspecialised as amœboid corpuscles, may specialise as muscular tissue, or cycle into the resting state, *i.e.*, develop into connective tissue (see fig. 19).

And if the cell cycle persist thus long in the life-history of the organisms, why should it disappear? In reality, it does not disappear completely. The amœboid corpuscles of the perivisceral fluid of an invertebrate—say an Echinus—develop, largely at least, from the ciliated epithelium lining of the cœlome—permanently exhibit, that is to say, one of the most characteristic phenomena of the cycle. And when under proper precautions we examine a fresh drop of the fluid, we observe the corpuscles as they die running together into a plasmodium,* so perfectly similar to that of a Myxomycete as actually to have been described by a recent observer as a new genus and species.† And this phase of the cycle takes place, in the so-called coagulation of corpusculate fluids of invertebrates generally.‡ Numerous other instances of the occurrence of some phase of the cell-cycle have been recorded, and have already been collected by the writer in a series of papers which have led to the present one; it is unnecessary to call attention to others, save perhaps the especially interesting announcement by Professor Haddon,§ of the occurrence of a plasmodial union of cells during the normal histolysis of Polyzoa.

* Geddes, "Observations s. l. fluide périviscéral des Oursins," *Arch. Zool. Exp.* VIII. † *Comptes Rendus*, t. lxxxii. No. 21.

‡ Geddes, "On the Coag. of Amœb. Cells into Plasmodia," &c., *Proc. Roy. Soc. Lond.*, No. 202, 1880, and *Trans. Roy. Phys. Soc. Edin.*, 1882.

§ Haddon, "On Budding in Polyzoa," *Quart. Jour. Micros. Sci.*, 1883.

Thus then it will be sufficiently evident that the morphological classification of tissues must be based upon the cell-cycle, the various permanent tissues being viewed as specialisations of one or other of its fundamental forms, or perhaps sometimes as synthetic types between them. And, finally, compressing the gist of several possible papers into as many passing allusions, it is evident that the theory affords us a basis for the criticism and compression of the recent literature—(1) of intercellular digestion (natural to the amœboid phase); (2) of that long dispute respecting the origin of the sexual elements of *Hydrozoa*, from ectoderm to endoderm (the cells of both of which show the cycle, and either layer thus develop ova or spermatozoa); (3) of the cœlome theory.

10. *Physiological Rationale of the Cell-Cycle.*—It is now time to demand some physiological rationale for this cycle, which has been hitherto regarded as of morphological interest alone. A mass of protoplasm anywhere is under constantly varying conditions—at one time receiving abundant energy from the environment, at another little or none. These variations are at least of three main kinds—(1) temperature, (2) light, (3) food. Thus, then a rhythm of more or less vital activity in definite relation to these conditions of the environment is inevitable.

It is unnecessary to remind the histological reader how often and how easily the existence of this rhythm is verified by actual observation. Every student is shown the intensification of amœboid or ciliary movement by heat, and its depression by cold or electric shock, and knows too the influences of various reagents or gases (*i.e.*, of modification of *food* in the general sense) in stimulating or retarding activity. The dependence on climate of the cell-cycle of the lower organisms, *e.g.*, *Protococcus* or *Amœba*, is familiar to every microscopist. The amœboid state varies widely with food and temperature; while the actual transition from the ciliated stage to the amœboid, and conversely, have been repeatedly observed; witness the papers of Hæckel, Lankester, and others including the writer.* They can only be viewed in fact as distinct from the morphological point of view; physiologically, they show but the extremes of one motile state.

* "On the Morphology and Physiol. of the Cell," *Trans. Roy. Phys. Soc. Edin.*, 1882.

Vast importance has been attached to the cellulose wall, as an assumed characteristic of plants, yet not only the cyst of a Myxomycete, but that of an Amœba, is now known to consist of cellulose. How is this cellulose wall to be accounted for? Why should the resting phase possess a cyst? What is the physiological rationale of this morphological characteristic of the resting phase?

Contracting muscle evolves carbonic acid and water, with evolution of heat; the quantity of heat and water products evolved diminishes as contractile activity diminishes; and this physiological common-place must hold true of every contracting cell, ciliated or amœboid. But contractility implies waste of formed materials, diminution of contractility therefore implies diminution of this disintegration of matter and dissipation of energy, of this combustion which we term waste. Cessation of contractility, therefore, involves cessation of the combustion of some product—of some fuel which was formerly required to maintain the process. *The cellulose wall which appears on the assumption of the quiescent state is thus the equivalent of the carbonic acid and water which were being formed and excreted during the state of contraction.* Being no longer required as fuel, it becomes itself thrown out as a waste product—which simply by reason of its chemical and physical properties—its insolubility and coherence—acquires at once its morphological permanence and its protective use.*

The applicability of this physiological conception to a new series of problems can here only be briefly hinted at. Without more than mentioning the discovery of Durin as to the formation of cellulose from cane sugar,† it may be briefly pointed out (1) that the occurrence of cellulose in Ascidians, or in pathological cases in the human brain, &c., is by no means unintelligible—the difficulty is rather the reverse—to explain why it is not invariably present in resting cells. These are never destitute of external intercellular substance, and the

* A vivid confirmation of the preceding theory of the origin of the cellulose wall has been suggested to me since the reading of this paper by my friend Dr Milne Murray, who reminds me that a quiescent muscle, instead of evolving carbonic acid and water, produces an enormous store of muscle-sugar or inosite, and that this is an isomer of cellulose, $C_6H_{10}O_5$. The same conception may throw light upon the physiological chemistry of other carbohydrates, such as glycogen, starch, &c.

† *Ann. Sci. Nat. Bot.*, 1877.

hypothesis thrown out many years ago by M. Frémy, our leading authority upon the chemistry of cellulose—that chitin and other analogous bodies really consist of cellulose linked with a proteid, seems well worth reviving. On this point the researches of Krukenberg,* especially are promising light.†

11. *Origin of the process of Sexual Reproduction.*—The plasmodial stage which terminates the cycle, seems in the first place little more than a mere mechanical union of cells exhausted by prolonged activity; in all normal cases it is soon followed by prolonged repose in the encysted state, and in the experiment upon invertebrate corpuscles, by quiescence and death. In the plasmodia of Protomyxa, Myxomycetes, and of invertebrate corpuscles alike, notably Echinus, the union is followed by a brief but extraordinary intensification of amœboid activity‡—the cause of which, as passing from cellular to protoplasmic physiology, must be discussed in a subsequent paper.

Some years ago considerable weight was attached by Sachs § to the hypothesis that the plasmodium formation of Myxomycetes might be regarded as a process of multiple conjugation. This view he now, however, withdraws,|| mainly on the ground that the nuclei have been shown not to coalesce as in true conjugation. It appears to me, however, that on the present theory the revival of that hypothesis, though in a somewhat different form, is inevitable.

No one doubts that the sexual elements of plants and animals are represented by the very slightly differentiated conjugating cells of *Spirogyra*, or the almost undifferentiated cells of *Mesocarpus.* With these the conjugation of two Amœbæ, two Actinosphæria or two Gregarines, are classified as a matter of course. But the recent observations of Gabriel upon the multiple conjugation of Actinosphæria, or of Gruber upon that of Gregarines, leave no doubt that in these cases at least conjugation may be multiple. The only difficulty is that offered by the non-coalescence of the nuclei. But even if there were any certain grounds for supposing that the essence of the process lies in the union of the nuclei, rather than in

* Krukenberg, *Vergleich. Physiol. Studien*, Bd. ii.

† *Ann. Sci. Nat. Bot.*, 1877.

‡ See figure of plasmodium of Echinus in author's papers in *Arch. Zool. Exp.* VIII.; *Proc. Roy. Soc. Lond.*, 1880, or *Trans. Roy. Phys. Soc. Edin.*, 1882.

§ *Manual of Botany*, 1st Eng. ed.

|| *Ibid.*, 2nd ed., Appendix.

the union of the protoplasm, we must expect on the evolution theory an incipient stage in which only the latter phenomenon should occur. That the nucleus is not invariable, much less indispensable, is of course evidenced by the existence of the Monera, or if their distinctness be questioned, we may appeal to the recent demonstration, apparently by the most refined histological appliances, that in young *Actinophrys* a nucleus is really absent,* and develops independently in adult life. Moreover, on the present view of the almost primordial nature of the Myxomycetes, their plasmodium is the only phenomenon which at all resembles conjugation, and since we have already viewed amœboid, ciliated, and resting forms as specialisations of the corresponding phases, it is no great extension of the theory to view conjugation as specialised from the plasmodial phase. This view will be strengthened when in the next paper we leave the cell-cycle to consider the physiological processes in the protoplasm itself.

12. *Relation between Normal and Pathological Tissues.*—Unless the step taken by Goodsir and Virchow—of regarding all pathological variations as ultimately expressible in terms of cellular structure and function, *i.e.*, of the cell theory, be deliberately retraced, we cannot avoid the application of the present re-statement of the cell theory to pathology. To do this in detail would, of course, require far more than the writer's knowledge, but a few brief and tentative suggestions may be put forward. Pathologists are reducing tumours to a common type—which seems essentially that of cell multiplication in the resting or encysted stage. It is certainly more easy to suppose, on the present view, that the appearance of a connective tissue tumour has been due to the placing of ordinary cells in new conditions favourable to the assumption of that phase of the ancestral cycle ; or from a slightly different point of view, to say that that inhibition of the cycle essential to the permanence of the whole organism has been locally removed, than, for instance, to suppose, with Cohnheim, the existence of a long dormant mass of embryonic tissue.

Again, we can easily modify the environment of living cells under the microscope—we can accelerate or diminish the activities of ciliated epithelium, by heat and cold, oxygen and carbonic acid, by alkali and chloroform. I have elsewhere † pointed out that the

* Gruber, *Zool. Anzeiger*, No. 118, 1882.

† *Op. cit.*, *Proc. Roy. Soc. Lond.*, 1879.

solution of the old dispute, as to whether the integument of certain planarians was amœboid or ciliated, was afforded by specimens of *Convoluta* which had been kept for many days in a shallow aquarium, scantily protected at nights from the cold of a severe winter. The normally ciliated cells of the ectoderm could be watched in actual progress of collapse into the amœboid state, and their cilia figured during their passage into psoudopodia (fig. 24). Here was a definite pathological change, in approximately known conditions, and distinctly in terms of the cell-cycle. Why should not a disorder of the ciliated epithelium of the bronchial passages be at least partly susceptible of essentially the same explanation? (fig. 25). May not the formation of pus be partly interpreted in terms of degeneration to the amœboid stage, and may not inflammatory changes be regarded as temporary and excessive intensifications of cellular activity, indicating a tendency to reversion to the amœboid state?

Whether these particular instances be acceptable to professed pathologists or not is after all a minor consideration, their aim has been merely to suggest that the phenomena of the cell-cycle—and particularly of those changes occurring under definite experimental conditions—may be applicable in their hands to fruitful research, not only in pathological histology, but in cellular physiology and therapeutics.*

Its adaptability to the treatment of physiological speculations is also obvious. Since the activities of the body are the aggregate activities of its component cells, not merely such phenomena as those of varying ciliary activity, but those of fatigue and sleep, of muscular and nervous tonus, and in fact every rhythm of increasing and decreasing cellular activity, become intelligible when viewed from this most highly generalised standpoint of physiology, as specialisations of that primeval cellular rhythm which lies before us in this life-history of the Protomyxomycete.

13. *Influence of the Environment upon the origin of Plants and Animals.*—One further physiological consideration may be briefly indicated, from its bearing on general morphology. The cell-cycle in its entirety is only possible in a fluid medium. Without water cilia cannot play, without fluid the amœba and the plasmodium must

* This conception is somewhat developed in the subsequent paper.

alike become stationary, and either dry up or encyst themselves. The cell-cycle in plants therefore is only found in its entirety in algæ. Archegoniates are indeed terrestrial, but their brief cell-cycle during fertilisation is absolutely dependent upon the abundant moisture, without access to which neither moss, liverwort, nor prothallium ever occurs. Thus it is that the higher terrestrial plants have become restricted to the encysted phase. Only to escape death, has the dryad become thus shut up within the tree; but once so protected the extensive replacement of the cryptogams by the phanerogams, in all the less humid climates of the world, is readily accounted for.

Passing to animal life, the vast preponderance of aquatic forms over terrestrial, is very similarly to be accounted for by the aid of the present theory. Only the higher members of a few groups have successfully emerged from their native element, and their existence depends upon their differentiation of an internal fluid medium, of that "milieu intérieur" upon which Claude Bernard was wont to lay such stress,* this in turn depending upon the early differentiation of internal cavities. The interdependence of morphological and physiological theory will be sufficiently obvious from such considerations.†

14. *Theory of Variation.*—The more completely one accepts and reflects upon the theory of natural selection, the more one feels the necessity for some view more satisfactory than heretofore of the causes of variation.‡ The present conception of the cell-cycle seems to go far towards supplying this. On the ordinary conception of the cell theory, that of the plant as an aggregate of encysted cells, and of the animal as an aggregate of essentially amœboid ones, the organism cannot be credited with any innate variability—its observed variations are merely those which it receives, so to speak, between hammer and anvil—from the forces of the environment. The present conception, however, of all cells, however varied and specialised, being essentially differentiations from an encysted, an amœboid or a ciliated form, and of these forms as phases of a single form-history, enables us to credit the cells and the resultant organism with an innate tendency to variation, and this along

* *Phénomènes de la vie communs aux an. et aux vég.*, Paris, 1879.

† "Morphology," *Ency. Brit.*, 'Rel. of Morphol. to Physiol.'

‡ *Cf. Origin of Species.*

certain definite and investigable lines. These modifications would still of course be largely determined by modification in the environment, yet the change of view is considerable. On the former view the organism is a plastic but essentially inert mass, yielding passively to the forces of the environment; on the latter, it is an active community, of which some or many members, under the influence of any favourable change of conditions, or the removal of any restraints, external or internal, immediately press into other positions and functions, which however apparently new, are either specialisations of the existing, or reversions to an earlier type.

Variation and disease are thus most closely akin; for since all variations are ultimately cellular, pathological changes are simply definable as those variations which happen not to be conducive to success in the struggle for existence. And thus we might proceed further and further with the discussion of ætiology.

The preceding theory then, although its range of application, unlimited in the scale of organic nature, may at first sight alarm the specialist, is actually founded on a simple but solid basis of observed facts; it has been seen fairly to meet and co-ordinate the very numerous and hitherto, for the most part quite unrelated problems which were enumerated at the outset, and even to be applicable to numerous minor and unexpected problems which these suggested. And thus, were it even viewed from the standpoint of mathematical probability alone, it has received the most overwhelming verification.

(*Explanation of the Plate at page* 292.)

II. An Hypothesis of Cell Structure.

1. *Statement of the Problem.*—Great attention has, especially of recent years, been paid to the problem of cell structure, and a vast body of observations have been accumulated. Of these many are generalised; many, however, still remain unco-ordinated, and an hypothesis which attempts at once to unify these, to throw light upon the structural and functional aspects of contractile protoplasm, and to unite all these with that theory of the cell-cycle above propounded, is therefore not untimely, and may, even if not completely exhaustive or satisfactory, be at least suggestive of a better explanation. Let us survey a few of the main peculiarities of protoplasmic structure which any such hypothesis must aim at unifying.

The lowest amœboid organisms are simply granular masses of protoplasm, but higher forms exhibit a differentiation of a hyaline zone of "ectoplasm" around a more fluid and granular "endoplasm." The immense variability of form, size, and general appearance present among the rhizopods has never been sufficiently allowed for; so that there is ample reason for doubting whether great numbers of described species have any real distinctness. Yet the elongated and reticulated, granular and circulating pseudopodia of the Foraminifera, and the radiating, clear, and far less contractile pseudopodia of the Heliozoa and Radiolaria present a most vivid contrast, which we have as yet no means of explaining. The remarkable changes presented by ova both before and during fertilisation,* and the doubtless fundamentally similar phenomena exhibited during cell division, require to be accounted for; while the long dispute as to whether the "granules" of protoplasm are really granules at all, or are the optical expression of the intersections of a stroma or network of denser protoplasm, cannot be omitted. Such a hypothesis must also aim at throwing light upon the mystery of muscular structure, and must also deal even with such apparently peculiar and exceptional phenomena as that "aggregation of the protoplasm," first described by Mr Darwin as occurring in certain cells of insectivorous plants † (which, when in active digestion, or when subjected to chemical, electrical, or even mechanical stimuli, exhibit an aggregation, or rather segregation of the protoplasm into two portions—the outer more or less hyaline, but containing irregular and constantly-changing streaks and granules of a more refracting and fluid substance, in which the colouring matter, when present, became accumulated).

2. *Statement of the Hypothesis.*—Darwin soon extended these observations to the protoplasm of root hairs, and went on to indicate its wide prevalence throughout the vegetable kingdom. His researches were verified and extended by Francis Darwin,‡ who showed that these granules did not consist of sap, as some vegetable histologists had suggested, but were essentially protoplasmic in their nature. It is the object of the present paper to apply these facts to

* Balfour, *Embryology*, vol. i.

† Darwin, *Insectivorous Plants*, London, 1875.

‡ *Quart. Jour. Micros. Science*, xvi.

the explanation of such problems of cell structure and contractility as those briefly enumerated above.

On this view, the granules of such a low vegetable organism as *Torula* (disregarding, of course, sap vacuoles and fat globules) are aggregation products, an assumption by no means excessive, especially when we bear in mind the activity of the chemical changes which are going on during its life and growth. But if this step be taken, we cannot resist regarding the Amœba in the same way; its granules too are aggregation products, and the clear ectoplasm, when present, may be viewed as protoplasm in which aggregation is not occurring. The variations of amœboid organisms in more or less granular character (a fact familiar to every observer) is thus brought into obvious relation with the state of nutrition, or with the quality and quantity of external stimuli; and its observed increase when stimulated, and its diminution during the resting state, are thus naturally accounted for. In the same way, in the granular pseudopodia of the Foraminifera, aggregation is in progress, in the hyaline processes of the Heliozoon not so. The granules of cells in higher animals may be, at least to a very large extent, similarly explained; while the disputes as to the presence or absence of a stroma become clearer when we bear in mind the fact that Darwin's aggregation-masses are at least as often greatly elongated or spherical, and that they may run in any direction, and unite or separate to any extent. The remarkable differentiations of protoplasm visible during cell-division, as exhibited by ova (of course excluding yolk granules, &c.), may not improbably admit of the same explanation.

3. *Contractile Structures—Muscle.*—The excessively difficult problem of muscular structure has not as yet received any widely-accepted solution, and even respecting matters of observation the widest discrepancies exist. In many invertebrates we cannot even be certain whether the muscles are striped or non-striped, so contradictory are the observations, while in a recent important paper by Professor Haycraft,* the homogeneity even of striated muscle is maintained. Brilliant light has, however, been lately thrown upon the arena of controversy by Professor Rutherford's recent elaborate demonstration † that the discrepancies in observation are largely

* *Proc. Roy. Soc. Lond.*, 1881.
† *Proc. Roy. Soc. Edin.*, 1883.

if not indeed altogether, to be explained by the fact that the different observers have studied their specimens in different stages of contraction. When fully extended, and then alone, the full complexity of the structure of striped muscle can be realised; with slight contraction Flögel's granules disappear, then Dobie's globules; finally, in completed contraction, the heads of adjacent sarcous elements come together, and the fibril is momentarily homogeneous, the former complexity reappearing on extension. So far Professor Rutherford's explanation—how does this come into relation with the present hypothesis? The doubly refracting portions of the muscle-fibrils may, on this view, be regarded as aggregation granules; for these must inevitably exhibit considerable regularity of form and arrangement, when we bear in mind that, if we admit the existence of muscle-fibrils at all, we imply that these possess a limiting surface,—of course tubular in form and ultra-capillary in fineness,—and still more so, if we assume with many histologists the existence of fixed points afforded by Krause's membrane.* In short, it is attempted to compare the aggregation-granules of a sundew, not only with those of an amœba, but even with those most complex and most peculiar differentiations of protoplasm observable in muscular tissue.

4. *Confirmatory Evidence.*—The present hypothesis is thoroughly in accordance with recent researches as to the nature and composition of protoplasm. Thus Brass† distinguishes cells into two layers,—the outer sensory, the inner nutritive, and describes phenomena which seem at least closely akin to aggregation.

Our knowledge of the development of muscle also supports the hypothesis. Thus, for instance, Wagener‡ shows that muscular fibres at first differentiate from the protoplasm of multinucleate cells, as perfectly smooth fibrils ("vollig glatte Fäden"), with interfibrillar substance. Later there arises, as a secondary differentiation, the refracting and non-refracting elements ("Isotropen and Anisotropen"), which can extend and diminish, also fuse together and again separate. In young heart-muscles these come and go under the observer's eye.

* *Cf.* Author's Prel. Note in *Zool. Anzeiger*, No. 146, 1883.

† Brass, *Zool. Anzeiger*, 120, 1882.

‡ G. Wagener, "Ueb. d. Entstehung. d. Querstreifen auf d. Muskeln," *Archiv f. Anat. u. Physiol.*, *Anat. Abtheil*, p. 543.

5. *Further Study of Aggregation—Cellular Therapeutics.*—High as is the importance of observations upon preserved tissues, the present hypothesis clearly points towards the importance of continuous observation of living cells when treated with various reagents—a line of research which Professor Frommann* is at present almost alone developing, and with such remarkable results. We must observe the effects, not of ammonic carbonate only, but of the whole pharmacopœia, and not upon the tentacles of Drosera merely, but upon vegetable and animal cells and tissues from the lowest to the highest; noting the changes which take place in all the structures and functions of the cell, and this, under all variations of temperature, light, electric state, and for various periods of time.

Of the practicability and interest of such an investigation only a single instance need be taken. When one treats an *Actinosphærium* with dilute ammonic carbonate, the most striking change results; its pseudopodia disappear, its complex protoplasmic structure vanishes; it loses its regular spherical shape, and collapses into an irregular granular amœboid mass with blunt pseudopodia—(the very likeness of the ancestral amœba),—and then soon breaks up.

And similarly there is little doubt that such a reagent would produce marked effect upon the epidermic cells of growing tadpoles,—a convenient means of research. Thus we set out from these researches of Mr Darwin upon a general investigation into what changes chemical substances produce upon cells,—an investigation which touches the general question of pharmacy and therapeutics in the most direct way, and which we may in fact speak of as cellular therapeutics. The interest of the admission of a drug does not end when it has been conveyed into the stomach, but really begins there. We must know what happens to the component cells of the organism,—we must, in short, observe the therapeutic effects of reagents upon the cells of vertebrates,—an investigation which points far. Such observations would not require constant but only frequent attention for long periods, and are thus perhaps especially suitable for the skilled pharmacist.†

* Frommann, "Untersuch. ueb. Struktur, Lebenserscheinungen u. Reactionen thier. u. pflanz. Zellen," *Jena Zeitschr.*, xvii. and sep. pub., Jena, 1884.

† *Cf.* Author's paper in *Jour. Pharmaceutical Soc. Lond.*, No. 714, 1884.

6. *Further Chemical Considerations.*—It is an observed fact that when amœboid cells unite into a plasmodium, there takes place the most remarkable intensification of the activities of the mass. The compound amœba seem possessed of all and more than all the activities of its component amœba—pseudopodia of the most extraordinary length and size are thrown out, and motion is far more rapid; in short, it would seem that not only are the activities of the component amœba summed but multiplied. The coalescing amœbæ may be regarded as serving as food to one another—their waste products and their surplus water are squeezed out and got rid of, and thus we can readily understand the summation of their activities. But how is this apparent multiplication of activity to be explained?

We have seen how carbonate of ammonia, an oxidised body isomeric with urea, is exceedingly stimulating to protoplasm; and Mr Darwin's researches have also shown that other alkaloids and waste products are excessively stimulating, and set up the most extraordinary aggregation; and that a poison, for instance, may act by excessively exaggerating this normal process. Here then is a use, not merely for the protoplasm, but actually for the waste products—the waste product of one cell acting as a stimulant when it meets the protoplasm of another. And from this consideration again new series of speculative applications radiate off in all directions. One may suggest that the use of the alkaloids in the coffee or strychnine or Calabar bean is not merely to protect the young embryo from being eaten by animals, but as a stimulant to germination. Or we may introduce the same conception into our speculations as to the uses of manures, in which the most valued constituents are precisely those salts which, like carbonate of ammonia, produce great aggregation.

Again, passing from the plasmodial union of cells to the probably derived union of ovum and spermatozoon, we cannot avoid imagining the latter bringing not merely a trifling contribution of additional protoplasm, but a store of substances especially stimulating to the vast mass of the ovum. And the identification above suggested of aggregation with the protoplasmic changes visible in the ovum after fertilisation, is thus seen to be by no means so improbable as might at first appear.

7. *Need of an Explanation of the Phenomena of Aggregation.*—

How is it that if we treat living protoplasm with certain reagents it breaks up into two substances? How are we to explain this observed fact? Is there any case known to chemists or physicists where a chemical reagent separates a substance, at first apparently homogeneous, into two distinct substances which afterwards reunite; or where an electrical or mechanical stimulus temporarily separates a complex mixture into its components? I am not aware of any parallel case; but the absence of an explanation underlying the phenomenon of aggregation itself is after all entirely outside, and subsequent to both the main thesis and the speculative corollaries of the present paper.

III. An Hypothesis of Contractility.

If we imagine a single drop of more or less fluid substance suspended in a surrounding medium with which it does not mix, its surface-tensions tend to keep it in a spherical form. This can of course be observed in a drop of oil or water, most conveniently in the well-known experiment in which oil is suspended in a mixture of alcohol and water of the same specific gravity. If now we interfere and elongate this drop, its surface tensions at once enable it to resume the spherical form, even against the resistance of the surrounding medium. It is inevitable to transfer this simple physical conception to explain the function of muscle. If the elongated components of the muscular fibre be more or less fluid (as we almost certainly know them to be, whether aggregation granules or not), they must needs also possess surface tensions; they must, therefore, also tend to shorten and broaden, and draw themselves into a sphere. And if all these multitudinous elements of the muscle are shortening and broadening, we have of course an explanation of that general shortening and broadening which we term the contraction of a muscle.

Moreover, just as the "contracting" drop of oil overcomes a resistance, so the "contracting" muscle overcomes a resistance equal to the sum of the minute resistances which the millions or thousands of millions of simultaneously contracting elements can overcome. Finally, an expenditure of energy must needs take place, and of this the "negative variation" of contracting muscle (perhaps of the contracting oil-drop also?) may afford the indication.

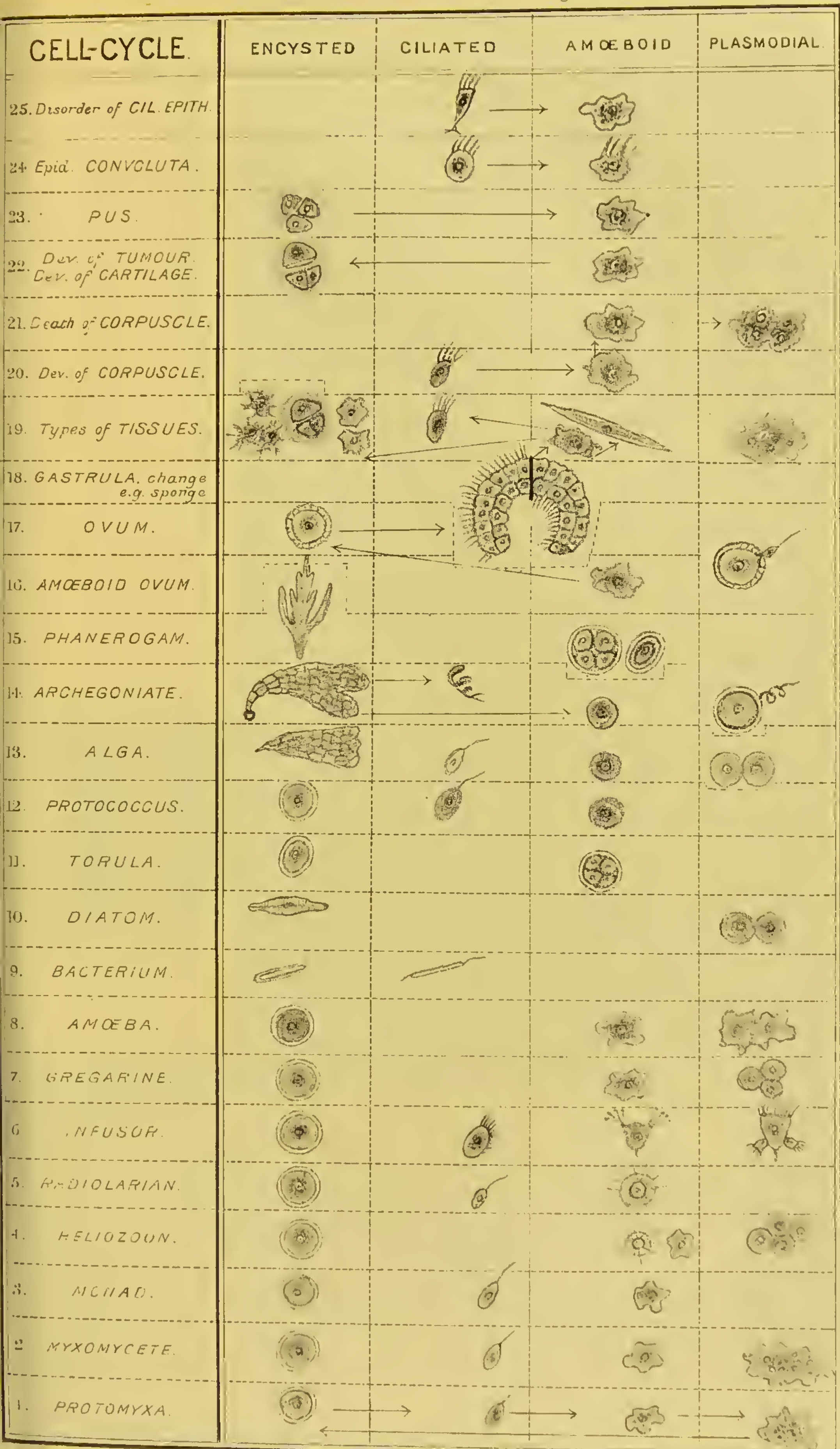
Be the latter suggestion valid or not, it is important to observe (1) that we have here (and for the first time so far as the writer is aware) an hypothesis which explains (*a*) the shortening and broadening of a contracting muscle, (*b*) its overcoming a mass resistance, in other words, that we have an explanation of the mode in which almost molecular movements are converted into movements of masses, a solution long sought by physiologists; and (2), that this hypothesis depends simply upon the more or less fluid nature of the essential muscular components, and is entirely independent of the acceptance or rejection of the hypothesis of the preceding paper, which suggests the identification of these muscular components with aggregation granules.

Explanation of Plate IV.

In columns allotted to the four stages of the cell-cycle (encysted, ciliated, amœboid, and plasmodial) are arranged the corresponding phases of the form-history of a few typical Protozoa and Protophytes, as also a series of diagrams illustrating the normal and pathological form-history of the cells of higher plants and animals. All are thus seen to be referable to the Protomyxan or Myxomycete type.

Among the Protozoa proper (figs. 3–8) the cell-cycle is almost complete; the encysted and amœboid stages are invariably represented. The plasmodial phase is of frequent occurrence: in Infusorians, Gregarines, and Heliozoa that of multiple conjugation representing it, and demonstrating its essential continuity with conjugation, *e.g.*, diatoms and algæ (figs. 10–13), and even with fertilisation in plants and animals (figs. 14 and 16).

Fig. 18 shows the cell-cycle in a developing gastrula, *e.g.*, sponge. In fig. 19 the various tissues are classified in relation to the cell-cycle; the connective tissues to the encysted, the muscular to the amœboid type, &c., even the plasmodial phase being represented during the histolysis of Polyzoa. Fig. 19 represents the development of an invertebrate amœboid corpuscle, and fig. 20 its formation of a plasmodium when drawn, while figs. 20–25 continue the application of the same theory to the explanation of pathological change.


CELL-CYCLE.
ENCYSTED
CILIATED
AMŒBOID
PLASMODIAL
25. Disorder of CIL. EPITH.
24. Epid. CONVOLUTA.
23. PUS.
22. Dev. of TUMOUR. Dev. of CARTILAGE.
21. Death of CORPUSCLE.
20. Dev. of CORPUSCLE.
19. Types of TISSUES.
18. GASTRULA. change e.g. sponge
17. OVUM.
16. AMŒBOID OVUM.
15. PHANEROGAM.
14. ARCHEGONIATE.
13. ALGA.
12. PROTOCOCCUS.
11. TORULA.
10. DIATOM.
9. BACTERIUM.
8. AMŒBA.
7. GREGARINE.
6. INFUSOR.
5. RADIOLARIAN.
4. HELIOZOUN.
3. MONAD.
2. MYXOMYCETE.
1. PROTOMYXA.